XXIX.—*On the Branchial Currents in the Bivalves.*

By William Clark, Esq.

To the Editors of the Annals of Natural History.

Gentlemen, Exmouth, September 1853.

I request permission to reply to Messrs. Alder and Hancock's comments in the 'Annals of Natural History,' vol. viii. p. 370. Pl. XV. N. S., on my branchial theory, which appeared in a paper on the *Pholadidæ* in vol. vi. p. 313 of that publication. I was so engaged last year in the examination of a splendid harvest of rare animals, that I had no time to consider their remarks, but having now an unlimited supply of *Pholades*, I will endeavour to acquit myself of my engagements with these gentlemen.

They commence by quoting parts of my theory, and say that I announce "that $\frac{9}{10}$ths, if not all, the branchial water is admitted by the pedal gape." On this point they observe—

"Let us for a moment consider what would be the consequence of Mr. Clark's supposition, that these animals obtain water only by the pedal gape. Nearly all of them pass their lives buried in sand or mud, or immured in solid stone, with only a small aperture externally, the pedal opening being beneath, and the siphonal tubes in communication with the sea. Yet Mr. Clark would have these animals receive only the small quantity of water charged with sand and mud that finds its way to the bottom of the cavity, rather than draw their supply from the pure element on the surface, by means of their long siphons."

To this quotation I reply, that a fresh and very extended examination of four species of the *Pholades* fully supports me in maintaining all my positions, and I think I shall demonstrate that Messrs. Alder and Hancock's system of branchial currents is erroneous. The only correction I have to make is, that I have clearly ascertained that the branchial, like the anal siphon, is both inhalant and exhalant.

With respect to their observations on the habits of the *Pholades*, it is only necessary to admit, that these animals often inhabit sand and shingle, mixed with clay, and are not always imbedded in hard rock. But we contend that the cavities in which they dwell afford sufficient passage for the sea water, and the areas of their habitats are saturated therewith, as when the tide withdraws, much of its waters is retained by the various strata, which by filtration reaches the burrows in a pure state, and not "charged with sand and mud."

Continual watchings for months of multitudes of these ani-

mals prove beyond doubt that the water is not only copiously received at the pedal gape or aperture, but is often expelled with as much force, and with a similar formed jet, as from the branchial siphon; and my dredger, who during the last fifty years has excavated more *Pholades* than any man in existence, says, that he continually sees the water expelled from the pedal gape. This is an important fact in corroboration of my theory, as an in- and ex-current is established pedally in combination with the branchial siphon.

I will now mention a decisive proof that nature, in all the bivalves, intends the water, under certain conditions, to be received and expelled by the pedal gape or aperture. When the gape of the *Pholas papyracea* is closed, by being domed by the animal, a large ovally dilatable fissure is always left for the water in the connecting membrane of the laminæ of the dome, in its centre, to correspond with the gape that has been rendered ineffective. And in the linear Solens, in which, from the quality of the foot and its singular position, the water cannot well enter pedally, a similar aperture is also left in the membrane of the connecting valves. In the *Myæ* and other bivalves the water can get access through the ventral and pedal apertures. Thus we learn from these examples that when nature has denied the ordinary pedal entry and exit for the fluid, she always supplies a compensation.

The periodic entry and reflux of the branchial water present two distinct characters; the one being regular, the other more uncertain. With respect to the first, place a dozen *Pholades* and as many *Pullastra pullastra*, or *P. decussata*, in a dish of sea water: it will be seen that each has a regular periodic action, the *Veneres* usually from one to two minutes, and the *Pholades* three to four, until a change of circumstances induces a new disposition. The entry and issue of the fluid, in conjunction with the pedal gape and aperture, are thus performed:—the animal simultaneously closes the orifices of both siphons, which after a short pause are again opened; the effete water flows from both, and fresh is received. But independent of these silent though very visible operations, there is about every five minutes a powerful and copious jet from both tubes, sometimes simultaneously, at others at intervals, and that from the branchial tube in the *Pholades* is almost always accompanied by a strong ejection from the pedal gape, and also in the *Veneres* from the pedal aperture, though from the absence of a gape in their shells it is not so visible. The periodic times of the in- and out-flux, of whichever character it may be, as the animal becomes exhausted, are more and more prolonged; they are only in vigour for twelve hours.

What is the object of these copious and regular receptions

and expulsions of water? Will not every reasonable person acknowledge that they can only serve for branchial purposes—the receptions, to administer water to the gill-laminæ, and the expulsions to remove it when effete by the contraction of the adductors of the valves and siphonal retractors? In corroboration of the above, I particularly refer to the Rev. James Bulwer's account of the *Isocardia cor*, published in the 'Zoological Journal,' vol. ii. p. 258. Messrs. Alder and Hancock cannot controvert these facts, and therefore in relation to my theory say, "This is, however, a special case having nothing to do with the regular branchial currents, as has before been pointed out to Mr. Clark."

My opponents may find their special case a general law, and their system of regular branchial currents an illusion.

They, having discovered that no ascertained communication—[this is a condition of my theory]—existed between the branchial and anal chambers, thus express the fact:—"We certainly find no opening between the foot and the gills, nor between the gills and the mantle;" and in consequence of their favourite doctrine being in jeopardy, they "found it necessary to make a careful examination of the anatomical structure of these animals," and have informed us of the discovery of a channel, by declaring the gill-laminæ and their interbranchial tubes permeable, on which—to them a most important fact, if true—they emphatically observe, "Thus in an instant the secret was explained; the currents communicate through minute openings in the laminæ of the gill-plates."

I think these gentlemen have formed an erroneous conclusion: I cannot accord with the monstrous position, that the impure branchial water, deprived of its oxygen by the cilia, and of the alimentary matters by the *palpi* of the animal, is sent by filtration, even if pores existed, through the gill-laminæ and interbranchial tubes, which are the supports of the delicate blood-vessels for discharge at the anal siphon.

As the capacity of the branchial chamber is at least three times greater than the anal, Messrs. Alder and Hancock must admit that two-thirds of its fluid is expelled agreeably to my theory; it is therefore difficult to conceive a plausible reason why a part of the effete water, only one-third, should be got rid of by an issue, termed by them a branchial current. The sustentation and aëration being unquestionably effected in the branchial vault, we may inquire, what is the object of this partial labyrinthine exit for the water instead of its being wholly ejected by the pedal aperture and branchial siphon, at which it entered, agreeably to the simple laws of nature?

In connexion with these views, I state a fact that may have

some weight even with the sceptical. The longitudinal retractors and transverse muscles of the siphons are of very great power; the office of the latter is to diminish the calibre of the tubes, that, in conjunction with the former, they may effect a more powerful expulsion of the impure fluid. As proof, if a dozen *Pholas dactylus* are placed in a large dish of sea water, they will cause so great an ejection from the siphons, not from the effect of sudden disturbance or being startled, but of regular periodical emissions, as to cover the table several times during the twelve hours of the day and also throughout the quietude of the night: assuredly this circumstance serves to prove that the impure water is thus expelled, and that no part of it permeates the interbranchial tubes.

However, it still appears that Messrs. Alder and Hancock insist on a regular in-current by the branchial siphon, and an ex-current from the anal, effected by *cilia*, for the use of the respiratory apparatus; these are, as I think, strange and impotent motor agents. I have in a former paper expressed a belief that the function of the cilia is to beat and subdivide the water, that the oxygen may be the more easily extracted. I must now observe that all the testaceous Mollusca have many parts of their bodies clothed with cilia, which show their action in a similar manner to the Bivalves; what then, in them, are the functions of these appendages? May we not reasonably conclude, the same as in the Bivalves, to extract air from the water not only for their branchiæ, but perhaps to pass the vital fluid through the pores of the body. One can hardly suppose that in either group their duty is mechanically to create currents, when a more simple, visible, and effective plan exists; I therefore think the view is untenable, that they effect the in- and out-flux of water in the anal and branchial chambers. I believe a simple hydrostatic law provides for this operation in all the Bivalves by a vacuum being formed by the contraction of the valves in the expulsion of the effete water, and that on opening them and relaxing the siphonal orifices to take in a fresh supply the vacuum ceases.

The action of the cilia is local. That they produce currents or rather eddies on the gill-laminæ and different parts of the body of the Gasteropoda cannot be doubted; these result from every stroke of each that causes a displacement of fluid which instantly reverts to its level, but they are not the locomotive agents of the entrance or exit of the branchial water; they are strictly particular, having no determinate line of operation, and act indiscriminately from every pole. As presumptive proof, examine an oyster or a mussel from a provincial stall a few days after they are received, when the cilia under the microscope will be found in full action as if just taken from the sea, and will continue so

as long as moisture remains. In this case these species, even if they had siphons, could not produce in- and out-currents by separate ducts, from non-access to water; we are, therefore, bound to give the preference to the idea that their functions are to eliminate the oxygen. I may observe, that cilia are attached to the different epithelia in all animals, from the monad to man. The inconsistency of such a motive power will be apparent from the consideration that the cilia must act antagonistically from opposite points; one set to work the water in branchially, and another to expel it through the anal duct after percolating the gill-laminæ and interbranchial tubes. I shall recur to the cilia, and expect to prove that the new scheme of communication between the two siphons is very problematical, I may say impracticable.

Messrs. Alder and Hancock go on to say, that any one may convince himself of the existence of a branchial in-current and an anal ex-current, by placing a *Pholas* "in a glass of sea water, and then by gently adding a little fresh, slightly charged with floating particles," he will perceive the two actions. I admit, by this process, that currents will ensue, as the invigorating fresh element causes the animal to expel that which has become effete and take in a new supply; but as I have, under every condition of experiment, examined multitudes of these creatures, I am bound to declare that the currents have no *continuous* regularity: and I think the mode of testing their presence by means of the water being charged with buoyant particles is fallacious; these only float on the surface, and are subject to many perturbations and deceptions arising from depth of water, currents of air, the position of the animal, whether on the ventral or dorsal surface, by its will and humour, state of exhaustion, and by an unnatural confinement. My repeated examinations show that the particles are whirled in all directions; sometimes they pass into the branchial chamber, at others none will enter: capricious gyrations, whether arising from the action of the animal or other natural causes, are their ruling character. With respect to the anal siphon, the floating particles are certainly repelled from its orifice in a somewhat regular and continuous manner, being only interrupted by the periodic reception of fluid to supply the exhaustions. The frequent repulsions of particles from the anal orifice have been construed by Messrs. Alder and Hancock to arise from the percolation of water from the branchial vault through the gill-laminæ and interbranchial tubes to an issue at the anal siphon, produced by the agency of cilia. I think it will appear that this complicated operation will meet with insurmountable difficulties, and though I admit the anal outflow, I protest against its being considered of branchial origin and regu-

lar; the regularity is fallacious, though most naturalists appear to have adopted that idea, without perhaps sufficient examination, and others have been careless in their observations. But the diligent observer of cause and effect will perceive that there is as much water inhaled as expelled by the anal siphon, and that its fluctuation in the branchial chamber, produced by the contraction and dilatation of the four gill-plates, which can often be seen by a lens through the orifice of a large *P. dactylus*, aided by the respiratory circulation, causes a pressure and an impulse on the interbranchial tubes; these, as before shown, are filled every two to four minutes by a reception of water anally, which after performing its function, of whatever nature it may be, is thus for a similar period made to reflow into the anal cavity, and from thence is discharged by an insensible contraction of the siphonal muscles until the exhaustion of the fluid: this is very evident by the failure of the current, which only recovers its full action on the periodic renewal of the water. I have thus, perhaps, explained the mystery of the so-called branchial current.

It is problematical what are the precise functions of the water that is received into the interbranchial tubes and anal vault; I have hereafter alluded to some of them conjecturally, and for the present will only observe, that as this tube acts as a conduit to the contents of the rectum, one probable use of the water is to break down and remove the dejections; and it would indeed be strange if it had no other entry, except from the branchial vault by the devious route of filtration through the interbranchial canals.

In further support of the view that the anal ex-current is not the effect of a percolation of liquid through the gill-laminæ, I will for a moment digress, and relate a short incidental experiment. As the anal siphon is somewhat longer than the branchial, it is easy to subject the latter to the influence of the water and isolate the former; it resulted, that whilst the water flowed into the branchial cavity, none, in an hour's constant observation under the lens, issued from the anal siphon, a sufficient proof of the non-communication of the two; but as soon as the anal siphon was allowed to reach the water and obtained a supply, the current recommenced.

I now come to another experiment from which Messrs. Alder and Hancock conclusively infer the connexion of the siphonal currents. They state, "that the nosle of a blowpipe charged with a coloured fluid was placed at the inhalant orifice of a *Pholas*, and immediately a quantity was drawn into the animal. Watching carefully the result, we had soon the satisfaction of beholding a blue-stained stream issue from the exhalant orifice."

To this I observe, that having tried the experiment again and

again, failure always occurred; as the animal, after receiving the coloured fluid, which was applied without difficulty, in general immediately discharged it by the pedal gape, or by the branchial aperture overwhelming with coloured matter both tubes, the orifices of which by their inflection by the animal were so retracted and blended together as to be undiscoverable; of course, any issue of liquid from a particular tube was undistinguishable. When, in any example, the fluid, which was coloured by archil, remained a little time without expulsion, I opened the branchial cavity to see if the gill-laminæ and interbranchial tubes showed any increased inflation or colour from the filtration of the injection, but no unusual appearance presented itself. I also opened the anal vault and collected with a camel's-hair brush as much of the moisture as possible; this was applied to a very small quantity of distilled water, but no trace of colour appeared; we may then presume that none of the injection had passed from one siphon to the other. But when the coloured fluid was administered anally, all the interbranchial tubes were at once filled and remained inflated more than an hour, representing minute well-filled hoses, which bore the pressure of a delicate wooden stylet, and exhibited the fluctuations of the liquid, which, on its removal, instantly reverted to the points of displacement without any escape into the branchial chamber. We may therefore conclude, that the interbranchial tubes are impervious tissues, and are supplied through the orifices of the crypts from the water sucked in by the anal siphon; and one of their uses is probably, by being filled, to afford a sufficient tension to the network of the blood-vessels that they may the better receive the action of the cilia: they may also possibly be the receptacles for the maturation of the ova, agreeably to the opinions of some naturalists; but in the multitudes I have examined I cannot corroborate this view, as during the months of May, June, and July I failed to see any deposit of ova either on the gill-laminæ, or within the interlaminar cavities, or in the crypts of the anal vault; still the "*genitabile tempus*" may be later; nevertheless the ovaria were well filled with germs of various sizes. Under all the circumstances of this experiment, I think, though it may not be impracticable, that it cannot be depended on even if the gill-laminæ are permeable; but as I confidently believe no communication exists through them, I must conclude that these gentlemen were mistaken in supposing they had detected an issue of coloured fluid from the branchial vault through their exhalant siphon.

I have now to consider the principal experiment, which Messrs. Alder and Hancock think will settle the disputed problem of in- and ex-currents in the Bivalves, produced by the action of cilia through separate siphons. They say,—

"But a simple experiment will at once solve this difficulty. Having killed a specimen of *Pholas crispata* with the siphonal tubes contracted as little as possible, and having placed it in diluted spirit a few hours to render the tissues firm without hardening them too much, we had again recourse to the blowpipe, charged as formerly with coloured fluid. The specimen was opened down the ventral margin, exposing to view the whole of the gills stretched along the roof of the branchial cavity. The nosle of the blowpipe was passed into the anal siphon, and on removing the finger from the top of the pipe, the contained fluid immediately filled the anal chamber behind the gills, and then passing at once down the tubes between the laminæ of the gills, issued through ten thousand pores, and dyed the water in the branchial chamber. Thus in an instant the secret was explained;—the currents communicate through minute openings in the laminæ of the gill-plates.

"Having thus satisfied ourselves of this fact, we next directed our attention to the structure of the gills. Accordingly the anal chamber was laid open, and its ventral wall was seen to exhibit four longitudinal rows of large orifices. These four rows of orifices, already well known to anatomists, correspond to the attached margins of the four gill-plates, which hang from the roof or dorsal membrane of the branchial chamber; this membrane being the ventral wall of the anal chamber,—the membrane, in fact, which divides the chambers.

"These orifices lead into wide tubes which pass between the two laminæ forming each gill-plate. These interbranchial tubes lie contiguous and parallel to each other, and extend the full width of the gill, being bifid within its free margin. Thus it is evident that the tubes within the gill-plates communicate freely with the anal chamber. The laminæ forming the walls of these tubes were now examined through the microscope, when the whole was observed to present a regularly reticulated structure composed of blood-vessels; those passing transversely being the stronger and more prominent. The longitudinal vessels, rather far apart from each other, form the meshes into parallelograms. These meshes are open spaces, fringed internally with a narrow membrane and active vibratile cilia. The two vascular laminæ forming the gill-plate are really sieves to separate suspended molecules from the surrounding medium on the passage of the water from the branchial to the anal chamber;—an apparatus of the most exquisite beauty and perfect adaptation to the desired end.

"We cannot understand how this beautiful structure escaped detection by the mercurial injection of Mr. Clark."

I at once dispose of the last remark to save trouble in my

counter-statement; if these gentlemen had read a little more attentively, they would have seen, in the paper on which they have passed their strictures, that Mr. Clark states, "the application of the mercury to that tube gradually filled the entire range of the branchial vessels, which exhibited a very elegant appearance, but no fluid escaped from them into the branchial sac."

It is proper to state, that the *Pholas crispata* is the species that has furnished my controversialists with their remarks on my branchial theory, which is illustrated chiefly by the *P. dactylus*. I am not aware that this circumstance is of much moment, as we may safely conclude that the gills of all the *Pholades* have in essentials the same character. But I ought to mention, that the framework of the respiratory apparatus in some tribes of the Bivalves presents a very different arrangement. For example, there are several British families whose species I have seen alive, and which fortunately can be obtained, that have a peculiar branchial construction, which appears as to *general* configuration closely analogous to that lately described in the 'Annals' to exist in the *Chamostrea albida* and *Myochama anomioides* of authors, but the *particular* parts of the mechanism in my species do not accord; I think the narrow reticulated ribands on the external surface are not permeable, and do not lie on apertures that communicate with the interbranchial tubes. I refrain, at present, from extending these remarks, but in a fitting time I shall be prepared with some comparative notes on certain species that have only a single complete gill-lamina and a rudimentary one on each side the body, which seem to me to differ essentially in structure from the descriptions that have been promulgated on the composition of the branchial mechanism of the species that have been alluded to.

I now enter on the counter-statement to the last quotation, and beg to observe, that Messrs. Alder and Hancock, in the explanatory sketch of their *Pholas crispata*, Pl. XV. vol. viii. N.S., give a very intelligible outline of their theory. Though entirely dissenting from it, I cannot but admire the ingenious delineation, particularly fig. 3. of the gill-laminæ, showing the aspect of the meshes; it has however one fault—it exhibits them *all* with symmetrical longitudinal fissures called "orifices," which I think are ruptures of the membrane of each mesh, not one of which exists naturally in the three species I have examined.

Since May 1853 I have often performed "the simple experiment" detailed by Messrs. Alder and Hancock in the third paragraph of their paper, p. 374; it is by far the most important of the series, as the problem of communication, with them, between the anal and branchial siphons, depends on it:—by the injections of more than 200 *Pholades* with mercury and coloured

fluids, the invariable result has been my inability, as in the first experiments in 1850, to pass the fluids through the anal chamber further than to fill all the interbranchial tubes; but I always found the gill-laminæ, which form their walls, impervious, instead of allowing liquid to issue "from 10,000 pores." It is necessary to state that the numerous interlaminar canals that compose the divisions of the gill-plates are nearly parallel, and hang vertically from the dorsal line, ranging at equidistances throughout a great part of the extent of each branchial plate, and by sutural lines of junction cut off the communication between each tube.

I will now enter a little more into detail on some points in connexion with the branchial laminæ, by describing the appearance of the areas of the parallelograms under repeated examinations by transmitted light, and also as opake objects, rendered so by the injection of mercury.

In a full-grown *Pholas dactylus*, the surfaces of each gill-lamina together comprise an extent of about a square inch, every one-tenth of which contains 400 oblong subquadrangular spaces, or 40,000 in each plate, forming a total in the four gills of 160,000; this admeasurement and enumeration may not be very far from the truth. In each parallelogram, besides a general suboval depression, there are within it five to twenty or more shallow excavations of various size and shape, but there is no ruling symmetrical fissure as delineated in Messrs. Alder and Hancock's fig. 3. Each area shows a plain, a pitted, and a mammillated or traceried surface, detected by the action of the microscopic foci. We will start from the plain surface in which there is certainly no perforation; the fine adjustment of the instrument measures the depth of the depressions, and by another movement shows the character of the minute points, thus proving that no fissure or aperture exists, as when there is really an imperfection in the membrane it cannot thus be resolved, but under every phase of the instrument the hiatus of a solution of continuity is seen. The shallow depressions are the uncovered patches of the membranous base of the scales or epithelium incident to all the Mollusca; from them the numerous vibratile cilia spring which present the most discordant and particular motions that operate from every point; sometimes they appear as if each entire pit was whirled on a vertical axis, at others a compact mass of strands dilates and contracts like the heart, then a fasciculus of cilia is seen beating the water with every irregularity; sometimes only a single cirrhus is raised and falls in quick succession, like a hammer in a mechanic's hand; but it is impossible to describe all the varieties of motion. In a fresh animal the action and strokes exhibit the greatest rapidity; it seems utterly impracticable that

regular currents can be formed by such a chaos of agency; rapidity and diversity is the natural character of the action of the cilia, and it is only by the exhaustion of moisture, which can never occur in natural sites, that a subdued and more deliberate motion is attained, and even then their direction is as variable as ever; I can only consider them as the eliminating mechanism of the oxygen. The epithelium is pretty regularly deposited on the upper area of a compound membrane, one lamina being thin, horny, and of a yellowish pale brown; the other thicker, of a more mucous quality and whiter colour: this is seen by examining the edges of a section. Between these membranes which form the substance of the gill-plates the network of the blood-vessels is spread, as without such support it would fall to pieces: perhaps the roots of the cilia pass through the epithelium and its supporting membrane, and impinging or centring on the coats of the blood-vessels, by a capillary or porous action supply them with the air they extract from the water. It is scarcely possible to view a more interesting object than the structure of the branchial mechanism and operation of the cilia, by transmitted light, under a power of 300 or 400 diameters. I think these data will almost convince naturalists that these organs cannot be the agents of a communication from the branchial chamber to the anal siphon.

It is necessary to state that occasional lesions, and now and then a perforation, are seen on the surface of the gill-laminæ, the evident effect of a casual imperfection; with these exceptions, entirety is the ruling aspect; all my fellow-observers concurred in this opinion; and two pieces of gill-lamina containing several interbranchial tubes were submitted to a distinguished metropolitan microscopist, who thus reported on them: "I can find no pores in them, unless a piece of leather may be called porous." Since this opinion a great number of the gill-membranes of the *Pholas dactylus* have been examined by transmitted light by one of Mr. Ross's microscopes, with the $\frac{1}{2}$ and $\frac{1}{4}$ of an inch object-glasses, a power more than sufficient to detect the presence of natural symmetrical apertures or pores through which *effective* permeation could be obtained; indeed that power would be equal to show pores through which no water could pass freely, and scarcely by exudation.

The gill-plates of the *Pholas parva* are more delicate than in the '*dactylus*.' No appearance of symmetrical apertures exists, but only an excessively minute wiry tracery, studded in the interstices with points, which, under a power of 300 linear, only presented a surface little larger than the point of the finest needle, and had the aspect of prominent dots rather than pores.

In the *Pholas papyracea* the gills are of the finest texture, but

exhibit no appearance of a permeable structure; minute points are scattered in the tracery of the parallelograms, some of them being circled by a shallow grooved line; but this is merely a depression of the epithelium or its supporting membrane. I have preserved the preparations. The *P. candida* has not been examined, and the *P. crispata* does not inhabit the South Devon coasts.

Having mentioned accidental lesions and gill-laminar imperfections, I have to add, that in testing Messrs. Alder and Hancock's chief experiment, no alcoholic injections should be used, as by their penetrating quality they may exude through these supereminently delicate tissues; nor should mercury be employed, as its weight in young subjects without great care often causes ruptures, and from its density it does not pass near so freely as aqueous fluids. Sea water coloured by indigo or archil, or pure, is the proper injection, which must not be pushed beyond a full distension of the interlaminar tubes. The animal should be prepared in as natural a state as possible, and not be killed by any process producing sudden asphyxia, as immersion in hot water or alcohol; the first destroys tenacity in delicate tissues, the second thickens and hardens them too much, and occasions lesions and fissures by contraction. There must be no lesions in the gill-laminæ, except those that result from imperfections, which prevail to more or less extent in every animal I have examined—at least 500; any solution of continuity at the junction of the gills with the excessively delicate membranes of the body will be fatal to success.

If the experiment is thus conducted, no injection through the anal siphon will flow into the branchial vault by the route of the interlaminar canals; the only moisture, if any, that can arrive there, may be a slight exudation, a proportionate one to the number of perforations and cracks in the membrane from laminar malformation, and of these only those which pass through into the interbranchial tubes. There may be in the 40,000 parallelograms in each gill, about twenty flaws or imperfections, and I reserve the possibility that all or most of these may arise from the manipulation of such delicate tissues.

After all these incidents, how am I to explain the great discrepancy between the experiments of the northern naturalists, illustrated by their "10,000 pores," and mine, by the impossibility of causing fluids to issue from the interbranchial tubes by percolation through the membrane on which the network of the blood-vessels is spread? But 't is said, the sight is keener in the North than with us southrons. The only solution I can offer is a mere guess, that the animals operated on by these gentlemen, after being killed, and alcoholized to harden the

fabric,—and the contractive qualities of alcohol are well-known;—had, when the moisture was evaporated, the membrane of the entire network of the branchial laminæ broken by lesions and contractions, and their fig. 3. in the plate has much the aspect of such ruptures. "I cast this idea on the waters," as Southey did "his little book," and it may have as much value as it deserves. I had scarcely written these lines when I found that my conjecture might be right. Having opened in a gill-plate an interbranchial tube that retained the injected mercury, I cleared it of the mineral, and being dry it was placed in water to recover pliability, for fixing on a tablet, on which it was carefully spread without stretching; I found that in the central portion of the membrane of the plate almost every parallelogram was ruptured, which under the microscope showed no previous solutions of continuity, and each fissure proved a *fac-simile* of those delineated vol. viii. N. S. Pl. XV. fig. 3.

The area of the portion of the plate examined contained about 2000 parallelograms in rows, and by its size caused the sphere of contractibility to centre in the middle, whilst towards the margins, a less resistance and greater elasticity prevailing, many of the rows of network preserved their integrity. I then prepared another portion of ten transverse and as many longitudinal rows; in this diminished area not a mesh was ruptured, and the membrane of the blood-vessels remained perfect. It appears then, that the moistening of the gill-plate with plain water—and of course with alcohol a much greater effect is produced—may have caused all the fissures in Messrs. Alder and Hancock's specimens, thus fully accounting for the singularly different results of our respective injections of the anal siphon.

If I am right in these points, the question of in- and ex-currents by cilia and separate siphons is disposed of. The data of these gentlemen to show a communication between the anal and branchial vaults through the membrane of the network of the gill-laminæ not being tenable, of course their theory falls to the ground, on the principle of "sublatâ causâ tollitur effectus;" consequently mine, as published in the 'Annals,' 1850, has not yet been proved incorrect.

Hitherto the *Pholades* have been more particularly the object of consideration; it may now be not amiss to turn our attention to a group of Bivalves which, though essentially the same, differ materially in the configuration and arrangement of many of their organs; they may perhaps assist us in searching out the truth, by the discordancy of their attributes with those of their precursors.

How am I to consider the *Anomiæ* and *Ostreæ*, that have open mantles and no tubes, in which the water must enter at every

point of the periphery that is patent, contemporaneously with the opening of the shell by the animal? Here the water cannot be passed off by what is called an anal tube, because none exists; it must therefore be discharged by the great ventral cavity. Or, am I to idealize, and suppose that in the same branchial vault a distinct in-current has its course and another out? I may observe, that in the Gasteropoda there is a similar periodic entry and expulsion of water from the branchial chamber as in the Bivalves; and after the cilia have extracted the oxygen, I have witnessed a hundred times the forcible expulsion of the effete fluid by a jet as decided as in them;—am I here also to suppose that there are two distinct opposite currents in the same undivided cavity?

I have now to inquire how the gill-percolation, admitting for argument that it exists, is disposed of in this tribe of Bivalves without siphons. If the water permeates the gills of the *Pholades*, it must do so in the *Anomiæ* and *Ostreæ*; in the former there is a possible vent by the siphon, but none in the latter, therefore it must revert to its source, the branchial cavity. Does not this go far to prove that there is no permeation in either case?

Then, may it not be permitted us, in this asiphonal group, without having recourse to an "*olla podrida*," or hash of currents, to conclude, that when the animal opens the shell for the admission of water to bathe the branchiæ, and when that function is accomplished, it ejects the effete fluid by the same channel it entered, as no separate duct can be found? Will not the calm consideration of this case make most men doubt the existence of branchial currents either by distinct tubes, that is one inhalant and branchial, and another exhalant and anal, or by what I term supposititious ones? The former position I think I have proved in the *Pholades* by showing that there is no effective communication between the two chambers; and in the *Anomiæ* and *Ostreæ*, the latter condition of the currents being imaginary, appears to be the most correct view. It may therefore be considered that in the Bivalves, whatever modification their siphonal mechanism may present, all are subject to a general law of the water being expelled from the same siphon or channel at which it entered, aided by the pedal gape and pedal aperture where they exist; and in the *Anomiæ* and *Ostreæ*, in which these organs are rudimentary or entirely wanting, the water is simply received and expelled through the ventral range, and not by an imaginative inhalant and exhalant regular current, effected by cilia.

The remainder of Messrs. Alder and Hancock's paper requires no further remark than a few words on their concluding experiment, showing how the colouring matters collect in the neighbourhood of the buccal aperture. I have obscrved these appear-

ances, but I am of opinion, that in an animal cut up from stem to stern, with the so-called in-current, as they admit, annihilated, little dependence can be placed on the action of the gill-laminæ floated in a shallow vessel, to account for the colouring matters seen at its oral termination. And I cannot understand the hydro-pneumatic statics of these gentlemen, nor the position agreeably to their theory, that "a tendency to form a vacuum" in the anal chamber and interbranchial tubes is effected by the "flowing out" of the water from the ex-current siphon, combined with ciliary agency, which actions, they add, are the foundation of their "correct answer to this question; How is the matter, divided into such minute particles, collected on the surface of the gills?"

But a fallacy with respect to a tendency to form a vacuum seems to present itself, as in this case a flowing out involves the idea of a flowing in, which militates against the vacuum, for the fact is, that with the outflow there is in their theory a contemporaneous succession of fluid to compensate any possible exhaustion. One would rather suppose that a tendency to a vacuum, instead of existing in the *anal chamber*, the point of issue, would be formed in the branchial vault, the source of supply, from a possible deficiency of fluid: a river shows no appearance of vacuity at its debouchure or elsewhere, whilst its sources maintain their integrity.

I can conceive in a running stream that the pressure of one portion of water on another produces an impulsion, not a vacuum; but how is this impulsion from mere declivity of gradient to operate in the Bivalves, in which the natural position of the siphons is almost invariably at an angle of 90° in reference to the horizon? How is the flow out of water to be effected in them? Are we called on to believe that the cilia, besides eliminating the oxygen for the blood, perform the function of a pumping apparatus? Surely I need not further entertain such an absurdity; we may therefore conclude that the water is expelled at intervals of two to five minutes from both chambers, by the powerful adductor muscles in combination with the siphonal retractors of the animal operating on the valves; these agents act as a *force-pump*; there is no other adequate exhausting mechanism.

I do not think the idea of ciliary currents, independent of those for the extraction of the oxygen, can be sustained. I also cannot admit, with my views of the impermeability of the gill-laminæ, that the concluding hypothesis of these gentlemen throws "some light on the sustentation of the Lamellibranchiate mollusks;" I believe the gills are strictly a respiratory machine, with the exception that they may be subservient in some or all

the Bivalves to reproduction. I consider that the *palpi* are the purveyors and locomotive agents of the alimentary matters.

As a last argument I submit a syllogism, which perhaps some of your readers will say, from its decisive character, had better have been placed at the head, instead of the end of this paper, and thus they and myself would have escaped the trouble of wading through long accounts of optical and other experimental tests.

In a gill-membrane in which cilia are planted, epithelium is always present, and it and its supporting tissue cannot exist without a membranous and *mucous substratum*; these are absolutely antagonistic to water and impermeable; therefore the gill-laminæ of the *Pholades* and other bivalves are impermeable.

I apprehend, that ciliated mucous membranes are neither absorbents nor emunctories, though the vessels of such glands may pass through them to the surface; they are probably a product by exudation from the blood-vessels, for the formation of an upper membrane and the epithelium. Thus the very constitution of the branchial plates informs the anatomist and physiologist, that there cannot through them be a communication from the branchial to the anal chamber.

It would be lost labour to prolong this disquisition, in which I fear my observations have been too often repeated, but the importance of the problem is my apology. If I have failed to convince, I have at least supplied matter for reflection, which may perhaps lead malacologists to doubt whether the doctrine of inhalant and exhalant currents by cilia and distinct apertures can be maintained against the evidence I have presented, and to admit that this long-entertained theory may prove a delusion.

I conclude with a remark of Sir William Napier, who thus offers an apology—all will exclaim, a needless one—for writing the history of what he terms "a thrice-told tale," the Peninsular War: the eloquent historian says, "that two men observing the same object will describe it diversely, according to the point of view from which either beholds it; in the eyes of one it shall be a fair prospect, to the other a barren waste, and neither may see aright."

Are the northern naturalists and myself in this category? He adds, "wherefore truth being the legitimate object of history, it is better that she should be sought for by the many than by few, lest for want of seekers, amongst false lights, she be lost altogether."

Let us then apply these views, and hope that in this branch of history many observers, besides the present controversialists, will step in to announce the truth and dispel the mists of prejudice.

I am, Gentlemen, your most obedient servant,

William Clark.